

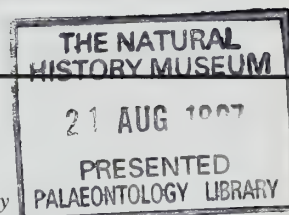
# The status of '*Plesictis*' *croizeti*, '*Plesictis*' *gracilis* and '*Lutra*' *minor*: synonyms of the early Miocene viverrid *Herpestides antiquus* (Mammalia, Carnivora)

MIECZYSLAW WOLSAN

Instytut Paleobiologii PAN, ul. Twarda 51/55, 00-818 Warszawa, Poland

MICHAEL MORLO

Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt am Main, Germany



**SYNOPSIS.** The reputed musteloid carnivorans '*Plesictis*' *croizeti* Pomel, 1847, '*Plesictis*' *gracilis* Pomel, 1853, and '*Lutra*' *minor* Lydekker, 1885 are recognized as junior subjective synonyms of the European early Miocene (Agenian) viverrid carnivoran *Herpestides antiquus* (de Blainville, 1842). The name '*Plesictis*' *gracilis* is a junior objective synonym of '*Plesictis*' *croizeti*, whose type locality is identified as Langy, of Agenian age, central France. The type locality of '*Lutra*' *minor* is Mainz-Mombach, of Agenian age, western Germany. The taxonomic histories of '*Plesictis*' *croizeti*, '*Plesictis*' *gracilis*, and '*Lutra*' *minor* are reviewed, synonymies are provided, and the holotypes described and figured.

## INTRODUCTION

The name-bearing types of the reputed musteloid carnivorans '*Plesictis*' *croizeti* Pomel, 1847, '*Plesictis*' *gracilis* Pomel, 1853, and '*Lutra*' *minor* Lydekker, 1885 constitute a part of the unique collections of The Natural History Museum, London. The specimens have not previously been adequately described, and only the holotype of '*Plesictis*' *croizeti* Pomel, 1847 has been figured. The taxonomic histories of the specific names given to them are highly confused.

The present paper provides comprehensive descriptions of the holotypes of '*Plesictis*' *croizeti*, '*Plesictis*' *gracilis*, and '*Lutra*' *minor*, and also reports the complicated taxonomic histories of these names, with evidence that they are all junior synonyms of the European early Miocene viverrid carnivoran *Herpestides antiquus* (de Blainville, 1842).

The following abbreviations are used in this paper: BMNH and NHM, Department of Palaeontology, The Natural History Museum (formerly British Museum (Natural History)), London; ICZN, *International Code of Zoological Nomenclature* (The International Commission on Zoological Nomenclature 1985); NMB, Natural History Museum, Basle; SMF, Department of Palaeozoology, The Senckenberg Research Institute and Museum, Frankfurt am Main.

## *PLESICTIS*' *CROIZETI* AND '*PLESICTIS*' *GRACILIS*

**TAXONOMIC HISTORY.** Pomel (1847) introduced the specific name '*Plesictis* *Croizeti*' to designate the partial mandible illustrated in fig. 5 of his pl. 4. Although neither description nor definition accompanied that name, it has nevertheless been made available by indication in accordance with Article 12 (b, 7) of the ICZN. Pomel's fig. 4 of pl. 4, as well as its reproductions published in Bronn & Roemer (1856: pl. 60, fig. 14b), Pictet (1857: pl. 4, fig. 8), and Viret (1929: text-fig. 3), represent the reversed mirror image of the original that is stored

in the NHM under register number 26702. As noted in the old vertebrate register at the NHM, this name-bearing type of '*Plesictis*' *croizeti* was purchased by the British Museum (Natural History) in June 1851 from 'M. Pomel' (M.J. Pomel according to Lydekker 1885: xiii).

In 1853 (reprinted in 1854) Pomel proposed the new name '*Plesictis* *gracilis*' for the partial mandible figured by him in 1847 under the name '*Plesictis* *Croizeti*', and he incorrectly applied the latter name to a skull of a mustelid carnivoran. Because both specific names were based on the same type specimen, they are objective synonyms according to Article 61 (c, iv) of the ICZN. The senior synonym, '*Plesictis*' *croizeti* Pomel, 1847, is the valid name of the taxon in accordance with the Principle of Priority (Article 23 of the ICZN).

The taxonomic status of '*Plesictis*' *croizeti* (= '*Plesictis*' *gracilis*) was further complicated by Filhol (1879a-b) who considered '*Plesictis*' *croizeti* and '*Plesictis*' *gracilis* to be distinct varieties of '*Plesictis* *robusta* Pomel, 1853, which is indeed a synonym of the musteloid carnivoran *Amphictis antiqua* Pomel, 1853. Although the type specimen of both '*Plesictis*' *croizeti* and '*Plesictis*' *gracilis* had already been figured or briefly described in Pomel (1847, 1853, 1854), Gervais (1852b, 1859), Bronn (1856), Bronn & Roemer (1856) and Pictet (1857), and the British Museum had been explicitly indicated by Gervais (1852b, 1859) as the institution where the holotype had been kept, Filhol (1879a-b) was, nevertheless, apparently unaware of its existence. At any rate, he made no mention of this specimen. Instead, he assigned a mustelid skull to '*Plesictis*' *croizeti* and two musteloid partial mandibles to '*Plesictis*' *gracilis*, believing that the characters of one of those mandibles, illustrated in fig. 5 of his pl. 22, corresponded to those of the holotype of '*Plesictis*' *gracilis* (his p. 128: 'J'ai trouvé dans la collection du musée de Lyon un maxillaire inférieur possédant des caractères correspondants à ceux que M. Pomel avait fait connaître comme devant servir à faire distinguer spécifiquement le *Plesictis* *gracilis*'). In addition, in his quotations of Pomel's (1853, 1854) descriptions of '*Plesictis* *croizeti*' and '*Plesictis* *lemanensis* Pomel, 1853, Filhol (1879a-b) mistakenly reversed the two descriptions, giving Pomel's

The mandibular foramen lies a little below the level of the alveolar border of the body, about 4.5 mm above the ventral border of the ramus and about 13 mm behind the alveolus for  $M_2$ . The foramen faces posteriad and somewhat laterodorsad.

$P_3$  and  $P_4$  are double-rooted, with the posterior root being larger than the anterior one. The base of the crown bears cingula anterobuccally and posteriorly on both teeth. The cingula are stronger on  $P_4$ ; much of the posterior cingulum of  $P_3$  has been broken away. The posterior cingulum of  $P_4$  is much better developed than the anterior one, which was also true for  $P_3$ , judging from the preserved base of its crown. The posterior cingular region of the base of the  $P_4$  crown is little deflected linguad.

The crown base of both  $P_3$  and  $P_4$  bears three projections arranged one behind the other anteroposteriorly to form a blade compressed buccolingually. The blade slightly curves linguad on the most anterior of the projections, the anterior accessory cusp, in both the premolars and on the most posterior projection, the posterior accessory cusp, in  $P_4$ . The middle cusp, the protoconid, culminates slightly anterior to the half of the tooth length and is distinctly largest, whereas the anterior accessory cusp is smallest. The anterior and posterior accessory cusps are stronger and larger relative to the protoconid on  $P_4$  than they are on  $P_3$ . The cusps are divided by prominent V-shaped notches on  $P_4$ . In both teeth, the tips of the anterior and posterior accessory cusps are noticeably worn away exposing the dentine. Wear has also broken through the enamel at the tip of the protoconid on  $P_4$ , but over a very small area only.

The crown of  $M_1$  is supported by two strong roots. There is no cingulum on the talonid, but there are two cingula running along the buccal base of the trigonid from the anterior end of the paraconid to the most anterior portion of the protoconid buccally and to that of the metaconid lingually. The buccal cingulum is very strong, whereas the lingual one is poorly developed.

The trigonid is notably arched buccad, making its lingual contour concave when viewed occlusally. The carnassial blade comprises the buccal ridge of the paraconid and the anterior ridge of the protoconid, which are divided by a deep, slit-shaped carnassial notch. The carnassial blade is rather deeply worn exposing dentine. The shearing surface on the buccal side of the paraconid and protoconid is considerably worn. Viewed from the occlusal surface, the carnassial edge of the paraconid abruptly turns anteriorly into a long, trenchant lingual ridge descending towards the metaconid from which it is set off by a valley. The carnassial edge of the protoconid curves posteriorly at an obtuse angle to continue into a sharp, partly damaged ridge that descends obliquely until it meets the metaconid. The anterior and lingual ridges of the protoconid delimit the lingual wall of this cusp, which flanks posterobuccally a deep, spacious valley that sets the protoconid off from the paraconid and metaconid. In addition to the anterior and lingual ridges, the protoconid exhibits a very short ridge, which is mostly worn away, on the base of its posterior wall. This short ridge ascends occlusolingual from the anterior end of the anterior edge of the hypoconid. There is an extensive wear facet on the posterior surface of the protoconid.

The metaconid is stout, well detached from the protoconid, and proportionally short anteroposteriorly. In lingual view, it resembles an isosceles triangle with its anterior and posterior profiles being slightly convex. In posterior view, the lingual contour of the metaconid is also slightly convex. A small part of the metaconid projects posteriorly beyond the protoconid so that its posterior edge is visible in buccal view. The slopes of the metaconid are angulated anteriorly, buccally, and posteriorly into ridges of which the buccal ridge is most trenchant or sharpened and the posterior one is most rounded or blunt. The anterior ridge descends towards the lingual ridge of the paraconid, from which it is separated by a valley. The buccal ridge is

united with the lingual ridge of the protoconid at a prominent, V-shaped notch. The posterior ridge meets the lingual wall of the talonid. The occlusal part of the posterior surface of the metaconid is worn.

Viewed occlusally, the posterior wall of the trigonid is almost straight, while the buccal and lingual contours of the crown are concave at the area where the trigonid meets the talonid. The buccal concavity is much better marked than the lingual one.

The talonid is deeply basined. Its buccal wall consists of an anteroposteriorly elongate hypoconid, which is the largest cusp on the talonid. The hypoconid is buccolingually wider and has its outer surface more inclined than is the case for the lingual wall of the talonid, making the talonid basin appear to be shifted linguad in occlusal view. Although wear has breached the enamel along the hypoconid, it is evident that the tip of this cusp was originally situated within the posterior half of the cusp length. The hypoconid is detached from the posterior wall of the talonid by a distinct V-shaped notch that is continued into an occlusobasal groove on the outer surface of the talonid.

The posterior wall of the talonid is lower than the buccal and lingual walls. It is somewhat worn occlusally and produced into three low, poorly differentiated elevations.

The lingual wall of the talonid forms two projections separated from each other by a notch. The anterior of these projections, the entoconulid, is small, whereas the posterior one, the entoconid, is much larger, being the second largest cusp on the talonid. The tips of both the cusps are worn, exposing dentine facets.

**TYPE LOCALITY.** Although Pomel (1847) did not indicate the place of collection of the name-bearing type of '*Plesictis croizeti*' explicitly, it is obvious from the contents of his article that the specimen had been excavated from Tertiary deposits in the region of Vaumas and Saint-Gérard-le-Puy (Allier, France). Several years later, Pomel (1853: 97, 1854: 61) expressly attributed that fossil to the Tertiary sediments of Langy ('Terrain tertiaire à Langy'), which is a village situated about 3 km west of Saint-Gérard-le-Puy and some 25 km southwest of Vaumas. Most subsequent authors listed the locality as 'Saint-Gérard-le-Puy'. It deserves to be noted, however, that the name Saint-Gérard-le-Puy has generally been applied in the literature to encompass various fossil sites discovered in several quarries in the region of the village Saint-Gérard-le-Puy, including the locality Langy as well (Cheneval, 1983).

The only published statements about the type locality of '*Plesictis croizeti*' that were significantly different were those of Gervais (1859) and Dawkins (1880a-b). According to the former author, the holotype of '*Plesictis croizeti*' was found in calcareous marls of Miocene age in the environs of Issoire in the department of Puy-de-Dôme (his p. 250: 'Fossile dans les marnes calcaires de l'étage miocène aux environs d'Issoire (Puy-de-Dôme)'). Dawkins in his statements (1880a: 386, 'Issoire, Volvic (Puy-de-Dôme)'; 1880b: 505, 'Issoire, Volvic, Puy-de-dome [sic]') simply quoted Gervais (1859). However, neither Gervais nor Dawkins presented any supporting evidence for their assertions.

Gervais's (1859) referral of the holotype of '*Plesictis croizeti*' to the locality Issoire is rather intriguing since that author was apparently familiar with Pomel's (1847, 1854) papers as indicated by their citations in his work, and since he studied that fossil during his visit to the British Museum (Natural History) shortly after it had been acquired by that institution, which is evident from footnote 2 on p. 11 in Gervais (1852b). In addition, one of the two labels on the type specimen of '*Plesictis croizeti*', which lies in its box and refers it to '*Herpestes croizeti*' (the only other label on the fossil is its register number), identifies the holotype as coming from the 'Upper

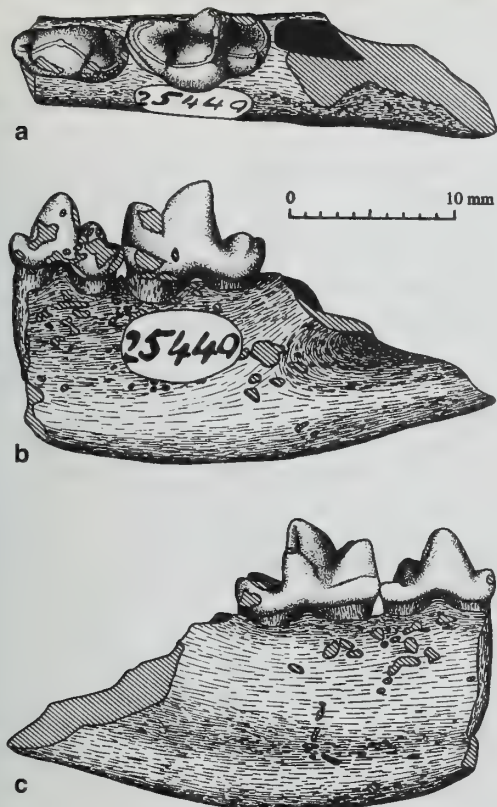


Fig. 2 The holotype of '*Lutra*' *minor* Lydekker, 1885 (BMNH 25449), a partial left dentary with  $P_4$  and  $M_1$ ; a, dorsal view; b, lateral view; c, medial view.

Oligocene' of 'Issoire, Puy-de-Dome [sic], France'. It is thus essentially consistent with Gervais's (1859) statement. There is no evidence, however, to support claim that just this label accompanied the holotype when it was examined by Gervais, or that the data included on it corresponded to those of any original but now lost label known to that worker. On the contrary, it seems to be more probable that the person who wrote the present label simply followed Gervais (1859), especially as both the old vertebrate register at NHM (which recorded Allier' as the locality of the holotype) and Lydekker (1885: 185) (who described it as 'the Lower Miocene of St. Gérand-le-Puy (Allier)') support Pomel's (1853, 1854) statement that Langy was the place where the type specimen of '*Plesictis*' *croizeti* was collected.

In conclusion, the correct name of the type locality of '*Plesictis*' *croizeti* Pomel, 1847 is Langy in the department of Allier, central France. The accurate placement of this fossil site is vague. Its age corresponds to the Agenian, early Early Miocene, as indicated by the exclusively Agenian occurrence of many taxa (e.g. *Herpestides antiquus*) attributed by Pomel (1853, 1854) to Langy.

## LUTRA' MINOR

**TAXONOMIC HISTORY.** Lydekker (1885: 195) applied the specific name *Lutra minor* to a '[f]ragment of the right ramus of the mandible, containing the last premolar and the carnassial; from the Lower Miocene of Mombach, near Mayence', purchased in '1850' by the British Museum (Natural History). He referred that specimen to

register number 25440. However, as seen from the vertebrate registers at NHM, the number 25440 has never been allocated. Instead, the old vertebrate register records under number 2544g, a '[f]ragment of lower jaw of *S[tephanodon]*, *minor*' with '2 molars *in situ*' from 'Mayence', purchased in 'Aug[ust]. 1850' from 'M. Becker'. The specimen BMNH 25449 is accompanied by two labels. One of them, which is glued to the fossil, displays its register number in which the '9' is of blurred appearance (see Fig. 2a–b), which may have been the reason for Lydekker's mistake. The other label, lying in the specimen's box, reads as follows: 'Fragmentary mandibular ramus[;] *Potamotherium minor*, Meyer sp.[;] Form<sup>n</sup> Lower Miocene[;] Loc<sup>y</sup> Mombach, near Mayence[;] Purch<sup>d</sup> 1850[;] Cat. 1, p. 149[;] Brit. Mus. Geol. Dept. 25449.' The reference to p. 149 in the first part of Lydekker's catalogue (1885) is an error, of course, because this page is actually devoid of any mention of this fossil; instead, the name of the ursoid carnivoran *Cephalogale minor* Filhol, 1879a is quoted there. Another inconsistency between Lydekker's (1885) account of '*Lutra*' *minor* and the data available on BMNH 25449 is that the latter represents the left branch of the mandible, and not the right one as indicated by that author. Otherwise, BMNH 25449 fits Lydekker's description exactly. Moreover, there is no other fossil in the collections of The Natural History Museum in London, which could represent Lydekker's specimen. Accordingly, we conclude that BMNH 25449 must be the specimen referred by Lydekker (1885) to *Lutra minor*.

Lydekker (1885) treated the name *Lutra minor* as a new combination for *Stephanodon minor*, deemed by him to be erected by Hermann von Meyer. However, Lydekker (1885: 195, footnote 1) 'ha[d] been unable to find a reference to this species'. The old vertebrate register at NHM refers the specific name *Stephanodon minor* to specimen 25449, but without any relation to von Meyer's name. Instead, this German palaeontologist is cited in the register in connection with number 25448 ('*Stephanodon monbachensis* [sic] V. Meyer') attributed to the holotype of *Stephanodon monbachensis* von Meyer, 1847, which is indeed a junior synonym of the arctoid carnivoran *Potamotherium valletoni* (Geoffroy Saint-Hilaire, 1833). According to the register, that fossil and three others catalogued under numbers 25450–25452 were purchased in August 1850 from M. Becker as coming from 'Mayence', exactly as specimen 25449. In all likelihood, all these fossils had been studied by von Meyer before they were conveyed to the British Museum. It is thus just possible that H. von Meyer gave the name *Stephanodon minor* to specimen 25449. At any rate, it is very probable that a label stating this name accompanied the specimen originally and was known to Lydekker. Its existence was explicitly stated by Pohle (1920: 17; 'Das Stück war von v. Meyer mit dem Namen etikettiert worden'), who, however, provided no evidence to support his statement. Regardless of this, even if von Meyer was really responsible for the name *Stephanodon minor*, as declared by Lydekker (1885) and followed by Trouessart (1885, 1897, 1904), Schlosser (1888), Pohle (1920), and Haupt (1935), he has not satisfied the criteria of availability of that name and therefore cannot be considered its author according to Article 50 (a) of the ICZN. Instead, Lydekker (1885), who satisfied these criteria through both publishing the name of this taxon and stating in footnote 1 on his p. 195 that 'this species [ . . . ] may be only a smaller form of [*Lutra valletoni*]', is the author of the name whose correct original spelling is *Lutra minor*.

The name-bearing type of '*Lutra*' *minor* has never been figured or adequately described in the literature. The only published information relating to its size and morphological characteristics is that of Lydekker (1885: 195, footnote 1) that '*Lutra*' *minor* 'may be only a smaller form of' *Potamotherium valletoni*. The subsequent authors confined themselves to following this assumption. Trouessart (1885,

1897, 1904) held '*Lutra minor*' to be a subspecies of *Potamotherium valletoni* while Pohle (1920), Haupt (1935), and Savage (1957) simply placed it in the synonymy of that species. Schlosser (1888: 123) expressly denied the specific status of '*Lutra minor*' ('Ebenso ist auch *Stephanodon minor* H. v. Meyer auf keinen Fall als besondere Art zu betrachten'), including it in *Potamotherium valletoni*, but later (1890) he quoted it as a separate species of *Potamotherium*.

The synonymy list of '*Lutra minor*' Lydekker, 1885 includes the following names:

- 1885 *Lutra minor* [or] [*Lutra minor*] Lydekker: xxi, 195, 266.  
 1885 *Stephanodon minor*; Lydekker: 195, 267.  
 1885 [*Lutra valetoni*] *minor*; Trouessart: 47.  
 1888 *Stephanodon minor*; Schlosser: 123.  
 1890 [*Potamotherium minor*]; Schlosser: 82.  
 1897 [*Potamotherium Valetoni minor*]; Trouessart: 281.  
 1904 [*Potamotherium valetoni minor*]; Trouessart: 212.  
 1920 *Stephanodon minor* [or] [*Stephanodon minor*]; Pohle: 16–17, 223.  
 1935 *Stephanodon minor*; Haupt: 38.  
 1957 *Potamotherium minor*; Savage: 155.

**DESCRIPTION OF THE HOLOTYPE.** The holotype, by monotypy, of '*Lutra minor*' Lydekker, 1885 is BMNH 25449, a fragment of a left dentary with partially eroded  $P_4$  and  $M_1$  (Fig. 2, Tables 1–3). The side-walls of the preserved fragment of body in the holotype dentary are convex in cross-section, excepting the ventral part of the medial wall where the surface of the dentary bone is somewhat depressed along the ventral border. The alveoli for  $P_4$ – $M_2$  are arranged one behind the other and closely spaced.  $P_4$  and  $M_1$  slightly overlap each other and have pairs of alveoli. Only the anterior part of the  $M_2$  alveolus is preserved; judging from this preservation, the alveolus was single and anteroposteriorly elongated. The masseteric fossa extends anteriorly to the level of the alveolus for  $M_2$ .

The morphological patterns of  $P_4$  and  $M_1$  are congruent with those of the corresponding teeth in the type specimen of '*Plesictis croizeti*', with the exception of the following differences concerning  $M_1$ : in the holotype of '*Lutra minor*' the lingual ridge of the paraconid is shorter; the lingual contour of the metaconid is slightly concave; the metaconid is somewhat deflected posteriad, making its posterior contour slightly concave when viewed from the lingual side; there is no crest on the anterior face of the metaconid, so that the anterior slope of this cusp is widely rounded and blunt; and, finally, no elevation could be detected on the posterior wall of the talonid. The crowns of  $P_4$  and  $M_1$  are generally less worn in the holotype of '*Lutra minor*' than those of the type specimen of '*Plesictis croizeti*'.

**TYPE LOCALITY.** The old vertebrate register at NHM reports the holotype of '*Lutra minor*' as having been collected in 'Mayence' (=Mainz). Lydekker (1885: 195) described it as coming 'from the Lower Miocene of Mombach, near Mayence' (now Mainz-Mombach), perhaps on the basis of an original, but now missing, specimen label. Lydekker's attribution is consistent with that on the label accompanying the holotype at present. Schlosser (1890), who knew both Lydekker's (1885) catalogue and H. von Meyer's unpublished drawings of carnivoran remains from Mainz-Weisenau (as seen from Schlosser 1887: 4, 6), referred '*Lutra minor*' (his *Potamotherium minor*) to 'Mainz (Weissenau)' (=Mainz-Weisenau). No evidence exists, however, to suggest that Schlosser's assignment concerned specimen(s) other than the holotype and, moreover, none of the copies of von Meyer's drawings preserved in NMB represents the type specimen of '*Lutra minor*'. Consequently, we conclude that Schlosser's *Potamotherium minor* pertained to the holotype of '*Lutra minor*', and hence its referral to the locality Mainz-Weisenau resulted from confusion.

**Table 1** Mandible measurements (in mm) of the holotype of '*Plesictis croizeti*' Pomel, 1847 and '*Plesictis gracilis*' Pomel, 1853 (BMNH 26702), and the holotype of '*Lutra minor*' Lydekker, 1885 (BMNH 25449).

	BMNH 26702	BMNH 25449
Distance between posterior-most points of $C_1$ and $M_2$ alveolar rims	31.9	–
Greatest distance between alveolar rims for $M_1$ and $M_2$	11.6	–
Length of $P_1$ alveolus (greatest diameter of $P_1$ alveolar rim)	2.0e	–
Width of $P_1$ alveolus (least diameter of $P_1$ alveolar rim)	1.0	–
Length of $P_2$ alveoli (greatest distance between rims of anterior and posterior alveoli for $P_2$ )	4.6	–
Width of $P_2$ alveoli (least distance from line connecting lingual-most points of $P_2$ alveolar rims to buccal-most point of these rims)	2.2	–
Length of $P_3$ alveoli (greatest distance between rims of anterior and posterior alveoli for $P_3$ )	6.0	–
Length of $P_4$ alveoli (greatest distance between rims of anterior and posterior alveoli for $P_4$ )	7.3	6.6e
Length of $M_1$ alveoli (greatest distance between rims of anterior and posterior alveoli for $M_1$ )	8.6	8.5
Length of $M_2$ alveolus (greatest diameter of $M_2$ alveolar rim)	2.6e	–
Width of $M_2$ alveolus (least diameter of $M_2$ alveolar rim)	2.2	–
Greatest horizontal distance between lateral and medial walls of dentary below $M_1$ perpendicular to long axis of dentary	5.6	5.8
Least distance from alveolar border of dentary between $P_3$ and $P_4$ to its ventral border, measured on medial side	9.3	–
Least distance from alveolar border of dentary between $M_1$ and $M_2$ to its ventral border, measured on medial side	10.5	11.7

'e' indicates an estimated value.

**Table 2** Measurements (in mm) of premolar teeth in the holotype of '*Plesictis croizeti*' Pomel, 1847 and '*Plesictis gracilis*' Pomel, 1853 (BMNH 26702), and the holotype of '*Lutra minor*' Lydekker, 1885 (BMNH 25449).

	BMNH 26702	BMNH 25449
Length of $P_3$ (from anterior-most to posterior-most points of crown)	6.2	–
Width of $P_3$ (greatest distance between buccal and lingual borders of crown perpendicular to antero-posterior length of tooth)	2.8+	–
Height of $P_3$ (least distance from occlusal-most point of tooth to basal margin of crown, measured on buccal side)	3.8	–
Length of $P_4$ (from anterior-most to posterior-most points of crown)	7.2	7.1
Width of $P_4$ (greatest distance between buccal and lingual borders of crown perpendicular to antero-posterior length of tooth)	3.3	3.4
Height of $P_4$ (least distance from occlusal-most point of tooth to basal margin of crown, measured on buccal side)	4.1	4.2e

'+' indicates a minimum measurement on an incomplete structure, 'e' indicates an estimated value.

**Table 3** Measurements (in mm) of  $M_1$  in the holotype of '*Plesictis*' *croizeti* Pomel, 1847 and '*Plesictis*' *gracilis* Pomel, 1853 (BMNH 26702), and the holotype of '*Lutra*' *minor* Lydekker, 1885 (BMNH 25449).

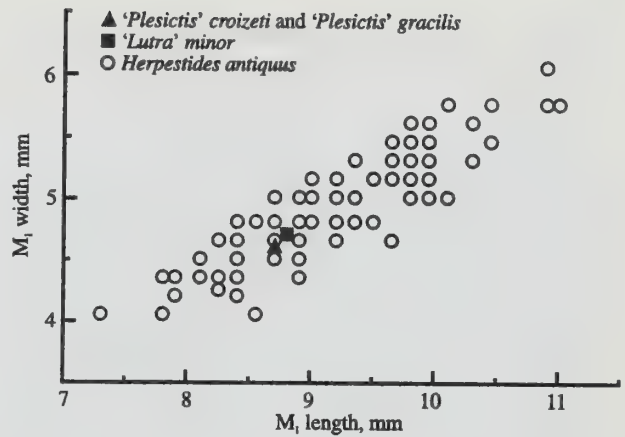
	BMNH 26702	BMNH 25449
Length (from anterior-most to posterior-most points of crown)	8.7	8.8
Width (least distance from buccal-most point of crown to line joining lingual-most points of paraconid wing and talonid)	4.6	4.7
Trigonid length (least distance from anterior-most point of crown to line connecting notch between protoconid and hypoconid with notch posterior to metaconid)	5.9	6.2
Least distance between buccal and lingual borders of crown across carnassial notch	3.8	3.7
Talonid length (least distance from posterior-most point of crown to line connecting notch between protoconid and hypoconid with notch posterior to metaconid)	2.8	2.6
Talonid width (greatest distance between buccal and lingual borders of talonid perpendicular to antero-posterior length of tooth)	3.7	3.7
Paraconid height (least distance from occlusal-most point of paraconid to basal margin of crown, measured on lingual side)	3.7+	3.8+
Protoconid height (least distance from occlusal-most point of protoconid to basal margin of crown, measured on buccal side)	5.1+	5.6
Metaconid height (least distance from occlusal-most point of metaconid to basal margin of crown, measured on lingual side)	3.7	3.6+
Hypoconid height (least distance from occlusal-most point of hypoconid to basal margin of crown, measured on buccal side)	2.3+	2.5
Entoconid height (least distance from occlusal-most point of entoconid to basal margin of crown, measured on lingual side)	1.9+	2.0+

+' indicates a minimum measurement on an incomplete structure.

To summarize, the correct name of the type locality of '*Lutra*' *minor* Lydekker, 1885 is Mainz-Mombach in Rhineland-Palatinate, western Germany. The exact location of this fossil site is uncertain at present. Tobien (1980) assigned the fossil fauna from Mainz-Mombach (his Mombach) to the *Hydrobia* beds of late Aagenian age, early Early Miocene.

## CONSPECIFICITY WITH *HERPESTIDES ANTIQUUS*

During their taxonomic history, '*Plesictis*' *croizeti*, '*Plesictis*' *gracilis*, and '*Lutra*' *minor* have been referred to various arctoid caniform genera, including the mustelids *Plesictis* Pomel, 1846, *Lutra* Rünnich, 1771, and *Mustela* Linnaeus, 1758 (for '*Plesictis*' *croizeti*; g. Gervais 1852b: 12), the amphictid musteloid *Amphictis* Pomel, 1853 (for '*Plesictis*' *gracilis*; Viret 1929), and the arctoid *otamotherium* Geoffroy Saint-Hilaire, 1833 (= *Stephanodon* von Meyer, 1847; for '*Lutra*' *minor*). However, the fact that they really belong to none of those genera needs no elaboration. Their name-bearing types differ from the characteristics of these genera in most aspects of their morphology, and more importantly, '*Plesictis*' *croizeti* = '*Plesictis*' *gracilis* and '*Lutra*' *minor* do not belong even to the border Caniformia Kretzoi, 1943, which is evidenced below.



**Fig. 3** A diagram of length versus width of  $M_1$ , showing the distribution of individuals in a sample of *Herpestides antiquus* from the Aagenian locality Montaigu-le-Blin in France (collection of NMB), compared to that of the holotypes of '*Plesictis*' *croizeti*, '*Plesictis*' *gracilis*, and '*Lutra*' *minor*.

As seen from the descriptions, illustrations (Figs 1–2), and measurements (Tables 1–3) presented in this paper, the holotype of '*Plesictis*' *croizeti* and '*Plesictis*' *gracilis* and that of '*Lutra*' *minor* differ only insignificantly from each other, plainly justifying the conclusion that they represent the same species. The available morphological features of that species unanimously point to its affiliation with the viverrid feliform *Herpestides* de Beaumont, 1967, known from the lower part (Aagenian) of the European Lower Miocene. According to de Beaumont (1967), that genus included the single, extensively variable species *Herpestides antiquus* (de Blainville, 1842). A comparison of the holotypes of '*Plesictis*' *croizeti* (and '*Plesictis*' *gracilis*) and '*Lutra*' *minor* with the corresponding portions of dentary and lower dentition of *Herpestides antiquus* from the French locality Montaigu-le-Blin, stored in NMB, revealed that both the morphological traits and size of the holotypes are well within the variability range observed in *Herpestides antiquus* (Fig. 3).

To conclude, on the evidence presented above we consider the name-bearing types of '*Plesictis*' *croizeti* Pomel, 1847, '*Plesictis*' *gracilis* Pomel, 1853, and '*Lutra*' *minor* Lydekker, 1885 to represent the species *Herpestides antiquus* (de Blainville, 1842). Accordingly, we synonymize the first three names with the last one that is the valid name of the species in conformity with the Principle of Priority.

**ACKNOWLEDGEMENTS.** Our sincere thanks go to J.J. Hooker (NHM) and B. Engesser, P. Jung, C. Mödden, and F. Wiedenmayer (NMB) for their aid and generous hospitality during our research at those institutions. This study was supported by the State Committee for Scientific Research (KBN) grant 6 P204 051 05, the Swiss National Science Foundation, the Alexander von Humboldt Foundation, and the German Research Association (DFG) grant Ro 143/12–1.

## REFERENCES

- Anonymous 1839. Marte fossile. *L'Écho du Monde Savant*, 5: 42–43.  
 — 1849. A. Pomel: Note über die im Allier-Dept. entdeckten fossilen Thiere. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1849: 872–874.  
 Bate, D.M.A. 1903. On an extinct species of Genet (*Genetta plesictoides*, sp. n.) from

- the Pleistocene of Cyprus. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, **1903** (2): 121–124.
- Beaumont, G. de** 1967. Observations sur les Herpestinae (Viverridae, Carnivora) de l'Oligocène supérieur avec quelques remarques sur des Hyaenidae du Néogène. Première partie. *Archives des Sciences*, **20**: 79–107.
- 1976. Remarques préliminaires sur le genre *Amphictis* Pomel (Carnivore). *Bulletin de la Société Vaudoise des Sciences Naturelles*, **73**: 171–180.
- Blainville, H.M.D. de** 1842. Des Viverras. In H.M.D. de Blainville, *Ostéographie ou description iconographique comparée du squelette et du système dentaire des Mammifères récents et fossiles pour servir de base à la zoologie et à la géologie*, **2** (1839–1864): 1–100. J. B. Baillière et Fils, Paris.
- Bonis, L. de** 1973. Contribution à l'étude des Mammifères de l'Aquitaine de l'Agénais. Rongeurs-Carnivores-Périssoctyles. *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série C*, **28**: 1–192.
- Bronn, H.G.** 1856. Fünfte Periode. Molassen-Gebirge. In H.G. Bronn & F. Roemer, *H. G. Bronn's Lethaea geognostica oder Abbildung und Beschreibung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Dritte stark vermehrte Auflage*, **3** (1853–1856, 6): 1–VIII + 1–1130. E. Schweizerbart'sche Verlagshandlung und Druckerei, Stuttgart.
- & **Roemer, F.** 1856. *Atlas zu H. G. Bronn's Lethaea geognostica oder Abbildung und Beschreibung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Dritte stark vermehrte Auflage*. E. Schweizerbart'sche Verlagshandlung und Druckerei, Stuttgart, 1850–1856. 123 pp.
- Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J.** 1992. Report of the RCMNS working group on fossil mammals, Reimsburg 1990. *Newsletters on Stratigraphy*, **26**: 65–118.
- Brünnich, M.T.** 1771. *Zoologiae fundamenta*. Copenhagen. 254 pp.
- Cheneval, J.** 1983. Les gisements de Saint-Gérard-le-Puy: 150 ans de paléontologie (1833–1983). *Revue Scientifique du Bourbonnais et du Centre de la France*, **1983**: 98–107.
- Cintract, R.** 1951. Catalogue des échantillons types et figurés des collections de paléontologie du Muséum National d'Histoire Naturelle. Mammifères. I. (Multituberculés, Marsupiaux, Primates, Tillodontes, Carnivores et Condylarthrés). *Bulletin du Muséum National d'Histoire Naturelle, Série 2*, **22** (Suppl. 1): 1–58.
- Dawkins, W.B.** 1880a. The classification of the Tertiary period by means of the Mammalia. *The Quarterly Journal of the Geological Society*, **36**: 379–405.
- 1880b. *Early man in Britain and his place in the Tertiary period*. Macmillan and Co., London. xxiv + 537 pp.
- Dehm, R.** 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge*, **58**: 1–141.
- Depéret, C.** 1887. Recherches sur la succession des faunes de Vertébrés miocènes de la vallée du Rhone. *Archives du Muséum d'Histoire Naturelle de Lyon*, **4**: 45–313.
- & **Douxami, H.** 1902. Les Vertébrés oligocènes de Pymont-Challonges (Savoie). *Mémoires de la Société Paléontologique Suisse*, **29**: 1–VI + 1–91.
- Fihol, H.** 1877a. Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des Mammifères. Seconde partie. *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, **16** (1): 1–338.
- 1877b. Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des Mammifères. *Annales des Sciences Géologiques*, **8** (1): 1–340.
- 1877c. *Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des Mammifères*. G. Masson, Paris. 561 pp.
- 1877d. Recherches sur les phosphorites du Quercy. *Thèses Présentées à la Faculté des Sciences de Paris pour Obtenir le Grade de Docteur ès Sciences Naturelles, Série A*, **26**: 1–561.
- 1879a. Étude des Mammifères fossiles de Saint-Gérard le Puy (Allier). (Première partie). *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, **19** (1): 1–252.
- 1879b. Étude des Mammifères fossiles de Saint-Gérard le Puy (Allier). *Annales des Sciences Géologiques*, **10** (3): 1–253.
- 1880. Étude des Mammifères fossiles de Saint-Gérard le Puy (Allier). (Deuxième partie). *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, **20** (1): 1–86.
- 1881a. Étude des Mammifères fossiles de Saint-Gérard le Puy (Allier). Seconde partie. *Annales des Sciences Géologiques*, **11** (1): 1–86.
- 1881b. Étude sur les Mammifères fossiles de Ronzon (Haute-Loire). *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, **24** (4): 1–270.
- 1882. Étude des Mammifères fossiles de Ronzon (Haute-Loire). *Annales des Sciences Géologiques*, **12** (3): 1–271.
- 1883. Notes sur quelques mammifères fossiles de l'époque miocène. *Archives du Muséum d'Histoire Naturelle de Lyon*, **3**: 1–97.
- 1889. Note sur les caractères de la base du crâne des *Plesictis*. *Bulletin de la Société Philomatique de Paris, Série 8*, **1** (1888–1889): 106–108.
- Gaillard, C.** 1899. Mammifères miocènes nouveaux ou peu connus de la Grive-Saint-Alban (Isère). *Archives du Muséum d'Histoire Naturelle de Lyon*, **7** (2): 1–79.
- Geoffroy Saint-Hilaire, [É.]** 1833. Palaeontographie. Considérations sur des ossements fossiles la plupart inconnus, trouvés et observés dans les bassins de l'Auvergne; accompagnés de notes ou sont exposés, les rapports et les différences des deux zoologies, celle des époques antédiluviennes et celle du monde actuel. *Revue Encyclopédique*, **59**: 76–95.
- Gervais, P.** 1852a. *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*, **1** (1848–1852): 1–VIII + 1–271. Arthus Bertrand, Paris.
- 1852b. *Zoologie et paléontologie françaises*. Planches XXVI, XXVII et XXVIII. Carnivores fossiles. In P. Gervais, *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*, **2** (1848–1852): 1–14. Arthus Bertrand, Paris.
- 1859. *Zoologie et paléontologie françaises. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe. Deuxième édition*. Arthus Bertrand, Paris. VIII + 544 pp.
- Giraud, J.** 1902a. Études géologiques sur la Limagne (Auvergne). *Bulletin des Services de la Carte Géologique de la France et des Topographies Souterraines*, **13** (1901–1902, 87): 1–410.
- 1902b. Études géologiques sur la Limagne (Auvergne). *Thèses Présentées à la Faculté des Sciences de Paris pour Obtenir le Grade de Docteur ès Sciences Naturelles, Série A*, **418**: 1–II + 1–410.
- Haupt, O.** 1935. Andere Wirbeltiere des Neozoikums. In W. Salomon-Calvi (ed.), *Oberrheinischer Fossilkatalog*, **9**: 1–103. Verlag von Gebrüder Borntraeger, Berlin.
- Helbig, H.** 1928. Carnivores des oberen Stampien. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft*, **47** (4): 1–83.
- Kinkelin, F. & Boettger, O.** 1903. Geologisch-paläontologische Sammlung. *Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*, **1903** (1): 82–101.
- Kretzoi, M.** 1943. *Kochictis centennii* n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Földtani Közlöny*, **73**: 180–195.
- Linnaeus, C.** 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Édition décima, reformata, **1**: 1–824. Laurentius Salvius, Stockholm.
- Lydekker, R.** 1885. *Catalogue of the fossil Mammalia in the British Museum, (Natural History)*. Part I. Containing the orders Primates, Chiroptera, Insectivora, Carnivora, and Rodentia. British Museum (Natural History), London. xxx + 268 pp.
- Mein, P.** 1990. Updating of MN zones. In E. H. Lindsay, V. Fahlbusch & P. Mein (eds), *European Neogene mammal chronology. NATO ASI Series, Series A*, **180**: 73–90. Plenum Press, New York.
- Meyer, H. von** 1847. [Untitled letter dated from] Frankfurt a. M., 4. Januar 1847. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **1847**: 181–196.
- Pictet, F.-J.** 1853. *Traité de paléontologie ou histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques*. Seconde édition, **1**: I–XIV + 1–584. J.-B. Baillière, Paris.
- 1857. *Traité de paléontologie ou histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques*. Atlas de 110 planches. J.-B. Baillière, Paris, 1853–1857. 77 pp.
- Pohle, H.** 1920. Die Unterfamilie der Lutrinae. (Eine systematisch-tiergeographische Studie an dem Material der Berliner Museen). *Archiv für Naturgeschichte, Abteilung A*, **85** (1919, 9): 1–247.
- Pomel, A.** 1846. Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. *Bulletin de la Société Géologique de France, Série 2*, **3** (1845–1846): 353–373.
- 1847. Note sur des animaux fossiles découverts dans le département de l'Allier. *Bulletin de la Société Géologique de France, Série 2*, **4** (1846–1847): 378–385.
- 1853. Catalogue des vertébrés fossiles (suite). *Annales Scientifiques, Littéraires et Industrielles de l'Auvergne*, **26**: 81–229.
- 1854. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier*. J.-B. Baillière, Paris. 193 pp.
- Redlich, K.A.** 1898. Eine Wirbeltierfauna aus dem Tertiär von Leoben. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abtheilung I*, **107**: 444–460.
- Roger, O.** 1887. Verzeichniss der bisher bekannten fossilen Säugethiere. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Augsburg*, **29**: 1–162.
- 1896. Verzeichniss der bisher bekannten fossilen Säugethiere. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Augsburg*, **32**: 1–272.
- Savage, R.J.G.** 1957. The anatomy of *Potamothereium*, an Oligocene lutrine. *Proceedings of the Zoological Society of London*, **129**: 151–244.
- Schlosser, M.** 1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, **6** (1888): 1–224.
- 1888. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden

- und fossilen aussereuropäischen [sic] Verwandten. II. Theil. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, **7** (1889): 1–164.
- 1890. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. III. Theil. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, **8** (1891): 1–106.
- Sherborn, C.D.** 1925. *Index animalium sive index nominum quae ab A. D. MDCCLVIII generibus et speciebus animalium imposita sunt. Sectio secunda a kalendis Januariis, MDCCCI usque ad finem Decembris, MDCCCL*; part VII: 1453–1771. British Museum (Natural History), London.
- Teilhard de Chardin, P.** 1915. Les Carnassiers des Phosphorites du Quercy. *Annales de Paléontologie*, **9** (1914–1915): 101–191.
- The International Commission on Zoological Nomenclature** 1985. *International code of zoological nomenclature. Third edition*. International Trust for Zoological Nomenclature, London; University of California Press, Berkeley. xx + 338 pp.
- Tobien, H.** 1980. Taxonomic status of some Cenozoic mammalian local faunas from the Mainz Basin. *Mainzer Geowissenschaftliche Mitteilungen*, **9**: 203–235.
- Trouessart, E.-L.** 1885. Catalogue des Mammifères vivants et fossiles (Carnivores). *Bulletin de la Société d'Études Scientifiques d'Angers*, **14** (1884, Suppl.): 1–108.
- 1897. *Catalogus mammalium tam viventium quam fossilium. Nova editio (prima completa). Fasciculus II. Carnivora, Pinnipedia, Rodentia I. (Protrogomorpha et Sciuromorpha)*, pp. 219–452. R. Friedländer & Sohn, Berlin.
- 1904. *Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementum, anno 1904. Fasciculus I. Primates, Prosimiae, Chiroptera, Insectivora, Carnivora, Pinnipedia*. R. Friedländer & Sohn, Berlin. IV + 288 pp.
- Villalta Comella, J.F. de & Crusafont Pairó, M.** 1944. Nuevos Carnívoros del Vindoboniense de la cuenca del Vallés-Panadés. *Notas y Comunicaciones del Instituto Geológico y Minero de España*, **13**: 55–88.
- Viret, J.** 1929. Les faunes de Mammifères de l'Oligocène supérieur de la Limagne bourbonnaise. *Annales de l'Université de Lyon, Nouvelle Série, I. Sciences, Médecine*, **47**: I–VIII + 1–328.
- Wenz, W.** 1921. *Das Mainzer Becken und seine Randgebiete. Eine Einführung in die Geologie des Gebietes zwischen Hunsrück, Taunus, Vogelsberg, Spessart und Odenwald*. Verlag von Willy Ehrig, Heidelberg. 351 pp.
- Wolsan, M.** 1993. Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). *Acta Theriologica*, **38**: 345–384.